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BOTANICAL GAZETTE

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OOGENESIS IN VAUCHERIA.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY. LXI.

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(WITH PLATES VI AND VII)

THERE have been published two accounts of the development of the oogonium of Vaucheria, attempting to explain in fundamentally different ways the final uninucleate condition of the structure at the maturity of the egg. All authors have found the young oogonium multinucleate, and the problem has concerned the history of these nuclei as the egg developed and the oospore matured. BEHRENS ('90), in partial agreement with SCHMITZ'S opinion that the material discharged from the opening of the oogonium represented a polar body, believed that the final single nucleus of the egg resulted from the fusion of numerous nuclei in the oogonium. KLEBAHN ('92, p. 237), in criticism of the results of SCHMITZ and BEHRENS, held that the egg and oospore were multinucleate. OLTMANNS ('95) came to very different conclusions. He described the gradual withdrawal of all the numerous nuclei found in the young oogonium from that structure into the main filament, with the exception of one which was left to become the nucleus of the egg.

The view of BEHRENS was in general similar to those of HUMPHREY and HARTOG for Saprolegnia, since the latter writers believed that the numerical reduction of the nuclei in this form was the result of successive nuclear fusions. The explanation of OLTMANNS has no parallel in any process of oogenesis known to the writer. Neither of these accounts seems to be correct, and the processes of oogenesis in Vaucheria are along very different lines, namely those of nuclear degeneration, which are in sympathy in all essentials with the events now known for gametogenesis in Saprolegnia (DAVIS '03), several members of the Peronosporales, and certain Ascomycetes.

These facts give a high degree of interest to Vaucheria, which becomes the greater in view of the position which this form takes in the phylogenetic systems of many authors as representing a possible point of origin of the Phycomycetes. This subject will be considered, with its bearings upon the writer's theory of the origin and evolution of the coenogamete, at the end of the paper, under the head of "Theoretical Considerations."

The material, identified as *Vaucheria geminata racemosa*, was collected at Chicago, the younger oogonia being abundant late in March and older stages a week or so later. Of the killing fluids employed, chromacetic acid after the formula of FLEMMING proved to be much the most satisfactory (1 per cent. chromic acid 25^{cc}, 1 per cent. acetic acid 10^{cc}, and water 65^{cc}). This formula is $\frac{1}{4}$ per cent. chromic acid and $\frac{1}{10}$ per cent. acetic acid. Chromic acid in excess of $\frac{1}{2}$ per cent. produced serious shrinkage. The weaker solution of iridium chlorid and acetic acid (Eisen) also gave fair results ($\frac{1}{2}$ per cent. iridium chlorid and 1 per cent. acetic acid). The cytoplasmic structure and plastids were perhaps better preserved in the latter fluid, but the nuclei did not stain so readily. All mixtures with osmic acid were objectionable, because the protoplasm of Vaucheria is filled with oils and fats which became so seriously blackened that they could not be thoroughly bleached. Chromic acid takes out much of these troublesome substances, or at least leaves the material so that it can be readily cleared. Paraffin sections were cut $5\,\mu$ thick and stained with safranin and gentian violet. The nuclei are so minute as to require the best of lenses, and the Zeiss apochromatic objective 1.5^{mm} with the compensating oculars was used entirely.

The oogonia are somewhat variable in number (2–6) and are arranged in a whorl near the end of short lateral branches just below the terminal antheridium. They commence their development as small protuberances which from the beginning are multinucleate (*fig. 1*). As growth proceeds the process enlarges and takes a globular form on the end of a short stalk (*figs. 2–4*). It is evident that the enlargement is accompanied by a stretching of the cell wall, which is always much thinner about the young oogonium than around the stalk and vegetative filament, a fact which is clearly shown in *figs. 4, 5, 6*, and *7*. The growth of the oogonium results from the accumulation of large amounts of protoplasm with numerous nuclei and chloroplasts, together with the formation of vacuoles which flow together, so that finally the protoplasm lies peripherally around a central space crossed by a few delicate strands and films of protoplasm.

The number of nuclei is variable, but always large; the range is probably from about 20 to 50. These nuclei are carried into the developing oogonium by the accumulation of protoplasm. They lie very close together at the tip of the young structure (*fig. 1*), but become scattered as growth proceeds, agreeing in this respect with the conditions found in all the growing points of Vaucheria. I have seen no indication of nuclear division in the oogonium, and am positive that it does not occur in stages as old or older than those shown in *figs. 2* and *3*. It is quite probable that mitotic figures are present in the vegetative branch before the development of the oogonia, but I have never seen the spindles. The nuclei are so very small and the plastids so numerous that studies of nuclear division in Vaucheria will be very difficult. It is important to note that there are no mitoses during the growth of the oogonium and none after its separation by the cross wall from the parent filament. In these respects oogenesis in Vaucheria is somewhat different from the processes as known in Saprolegnia and the Peronosporales, where there seem to be always one or two general mitoses after the oogonium is formed. The absence of nuclear divisions during oogenesis in Vaucheria presents serious difficulties for the theories of some authors that such mitoses indicate reduction phenomena in those fungi where they have been most studied. These speculations have been recently criticised by the writer (DAVIS '03, pp. 339–342) and the subject will be further considered later in this paper.

We will now describe he development of the cross wall by which the oogonium is separated from the parent filament. It appears when the oogonium is about two-thirds its mature size. The wall is laid down between two plasma membranes, as was shown by HARPER ('99) for the formation of sporangia in Pilobolus and Sporodinia, and by DEAN SWINGLE ('03) in Rhizopus and Phycomyces. The plasma membranes are formed chiefly along the surfaces of flattened vacuoles. I have seen no evidence of furrows cutting inward from the surface as takes place in Pilobolus and Rhizopus, but such structures would not be seen easily in Vaucheria because the stalk is rather narrow. *Fig. 4* illustrates an arrangement of vacuoles at the base of an oogonium which would probably have determined the position of the cross wall, and *fig. 5* shows a more advanced condition when the plasma membranes have definitely separated from one another. The stages shown in *figs. 6–8* are all somewhat older than that of *fig. 5*, and there is evidence in all of them that the wall has began to form as a delicate film visible at certain points between the two plasma membranes.

The oogonium at the time of the formation of the cross wall is multinucleate. There is no evidence in my material of the withdrawal of nuclei from this structure, as described by OLTMANNS, before the wall is laid down, and my preparations indicate that the oogonium contains as many nuclei immediately after the formation of the wall as before. These conditions are shown in *figs. 5–7*. The number of nuclei is always large, but is variable, ranging from 20 to 50. They may be readily demonstrated at this period when properly stained, but are very difficult to trace from this stage of development onward because of the remarkable and rapid nuclear degeneration which sets in at this time. This interesting phenomenon is apparently exactly the same as that which takes place at closely corresponding periods of oogenesis in Saprolegnia and in several of the Peronosporales.

The degeneration of the nuclei really begins a little before the oogonium is separated from its parent filament. At that time the nuclei in the oogonium do not stain as strongly as those in the antheridium and in neighboring portions of the vegetative filament. The nuclear membrane is less distinct and there is very little substance in the nucleus except the large nucleolus. *Fig. 9* presents a series of nuclei from the same section of which *fig. 7* is a single oogonium. In *fig. 9*, *a* is a nucleus from the antheridium, *b* from a region of the branch slightly below the antheridium, *c* from near the oogonium, and *d* from within an oogonium. It will be seen that *a*, *b*, and *c* are nuclei which, although small (magnified 2,000 diameters), present the structure of the nuclei of higher plants; that is, each has a nucleolus lying among granules of a chromatic nature and linin. In *c* these structures are less conspicuous than in *b*, while *d* shows unmistakable signs of degeneration, for its nuclear membrane appears very faint and there is scarcely any trace of chromatin or linin. The nucleolus, however, is generally large and stains deeply and is always the last structure in the nucleus to disappear. *Figs. 6* and *7* show degenerating nuclei in oogonia shortly after the formation of the cross wall.

It is very difficult to trace the degeneration and final dissolution of the numerous nuclei in the oogonia, because we are dealing with structures that become more and more difficult to stain and find. It becomes in the end impossible after the nuclear membrane disappears and the nucleolar material is scattered throughout the cytoplasm. These baffling conditions are identical with those in the oogonium of Saprolegnia which the author has recently described (Davis '03, p. 239).

The mature oogonia are finally uninucleate. There seems to be no doubt of this condition, and the factors governing the selection and survival of the fortunate nuclei are of interest. We know that the process in Saprolegnia (Davis '03, p. 239–243) is intimately connected with the presence of organized structures in the protoplasm, the coenocentra, which are probably the morphological expression of dynamic centers. I have not been able to find a coenocentrum in Vaucheria. It is possible that the plastids might obscure such a structure, but this is not likely unless it were very small. But there are conditions around the surviving nucleus in the oogonium which closely resemble those of the Saprolegniales and Peronosporales.

Before the formation of the cross wall the protoplasm in the oogonium is arranged quite irregularly. There is always the rather thick peripheral layer just inside the cell wall, but the interior region generally contains several irregular vacuoles which frequently open into one another. These conditions are partially shown in *figs. 3–5*, but of course they can be understood only by the examination of a number of consecutive sections.

After the formation of the cross wall, the arrangement of the cell contents becomes more regular. The oogonium increases rapidly in size, and the peripheral layer of protoplasm grows proportionally thinner. The strands and films of protoplasm that before crossed the oogonium irregularly become arranged so that there is a gradual accumulation of the protoplasm in the center of the cell, held in position by delicate strands which pass to the periphery, and the surviving nucleus always lies within this region. *Figs. 10–12* illustrate these conditions as they appear in thin sections (5 μ), but they cannot show the numerous radiating strands that hold the central mass in place. The degenerating nuclei lie chiefly in the peripheral layer of protoplasm, but some may always be found in the larger strands that enter the interior of the oogonium.

Although I have not been able to find any morphological evidence which would indicate that this accumulation of protoplasm is a dynamic center of the cell, there are good reasons for thinking that it really is such. The surviving nucleus of the oogonium is always found in this central mass surrounded by plastids and deeply staining granular protoplasm, which suggests material of a trophoplasmic nature. The peripheral protoplasm forms a thin layer under the cell wall in which one may find for a long time traces of the other nuclei that have degenerated. *Figs. 10* and *11* show some of these nuclei (*d*) so far reduced that there is nothing left but a deeply stained (with safranin) globule of nucleolar material apparently lying free in the protoplasm. No one would relate these structures to nuclei unless he had followed their history through the process of degeneration, for they are soon reduced almost beyond the point of recognition. But at this time the surviving nucleus (*fig. 10*) near the center of the oogonium increases rapidly in size until in the mature egg (*fig. 11*) it is three or four times as large as the original nuclei in young oogonia. The inference is plain that the central region of the oogonium is a much more favorable situation for nuclear growth and activities than at the periphery.

For this reason the author considers the dense central mass of protoplasm as comparable to the region of the egg in Saprolegnia and the Peronosporales which is dominated by the coenocentrum. It is apparently the region of the cell most favorable for nuclear growth and activity, and as such is a dynamic center. There is a very close resemblance to certain of the Peronosporales (*e. g.*, Pythium) whose oogonia have merely an accumulation of dense protoplasm in place of the usual well-defined coenocentrum.

The growth of the surviving functional gamete nucleus presents some interesting features. There is a marked increase in the amount of chromatin which fills the interior with numerous small granules on a very delicate linin network. The nucleolus does not increase in size, so that it appears relatively much smaller in the older nucleus than in the younger (compare *fig. 11* with *figs. 3* and *4*). *Fig. 11* is of an oogonium almost at maturity, and *fig. 12* is after fertilization and shows two gamete nuclei fusing and also the remains of three sperms which were unable to enter the egg.

The final steps in the maturation of the egg, as has been frequently described, consist in the breaking down of a portion of the wall of the oogonium and the formation there of a pore through which the sperms enter. Much slime is developed, which partially exudes from the opening. Numerous sperms are attracted to the oogonium, and one may frequently find conditions such as are shown in *fig. 13*, where the slime at the opening is filled with sperms held in the mucilaginous matrix. It is possible that such conditions were interpreted by Schmitz as nuclear material thrown off from the egg as a polar body.

The union of the gamete nuclei takes place slowly. The male nucleus increases greatly in size, apparently being nourished in the dense central region of the egg, and the great increase in the amount of chromatin is as conspicuous here as in the female nucleus. Although the male nucleus is much smaller at first than the female, the two are approximately the same size before they begin to fuse (*fig. 14*), and both show essentially the same structure at that time. As fusion proceeds the two nuclei become indistinguishable (*fig. 12*).

The history of oogenesis in Vaucheria may then be briefly described as from a multinucleate gametangium, by a process of rapid and complete degeneration of all the nuclei except one, which is reserved with all of the protoplasm for a single uninucleate egg. In these respects Vaucheria offers certain important differences and yet some fundamental points of agreement with the conditions in the Saprolegniales and Peronosporales, which will now be considered.

THEORETICAL CONSIDERATIONS.

The essential agreement of the processes of oogenesis in Vaucheria with those of Saprolegnia and members of the Peronosporales is most striking. The oogonium in all of these forms so far known—Vaucheria, Saprolegnia, Pythium, Peronospora, Plasmopara, Sclerospora, Albugo, and Araiospora (KING '03)—is differentiated from the parent filament as a multinucleate cell. There may be one mitosis in the oogonium (Saprolegnia), or two as in certain of the Peronosporales, or there may not be any (Vaucheria), but finally extensive nuclear degeneration always begins. From among the weakened nuclei one or more are selected to preside over the eggs. The position of these surviving gamete nuclei in relation to favorable dynamic centers of the oogonium determines their selection and leads to extensive regenerative growth. In Saprolegnia and some of the Peronosporales (*i. e.*, Albugo, Peronospora, Plasmopara, Sclerospora) the dynamic centers are marked by the protoplasmic structures called coenocentra, which are apparently trophoplasmic in character, since they exert a chemotactic influence on the gamete nuclei near them and are obviously concerned with their later growth. Although there is no coenocentrum in Vaucheria, the surviving nucleus takes its position in a central mass of protoplasm which is evidently the most favorable situation in the oogonium for its growth, and as such is a dynamic center, although there is little morphological evidence of the condition.

The fact that there are no mitoses in the oogonium of Vaucheria is seriously against the view that they have relation to reduction phenomena when present in the oogonia of Saprolegnia and the Peronosporales. I have already expressed the conviction (DAVIS '03, pp. 339–342) that these mitoses in the oogonium have no such significance, because they are so variable in their appearance and because there is no positive evidence of such functions. ROSENBERG ('03) from studies on Plasmopara believes that a synapsis condition preceding the first of the two mitoses in the antheridium and oogonium of this form indicates reduction phenomena comparable to that in the tetrad division of the spore mother-cell of higher plants. The author has recently (BOT. GAZ. **36**:154–155. 1903) criticised this view in several respects, which need not be repeated here, and the absence of mitoses in Vaucheria offers further difficulties for such a theory. RUHLAND ('03) is also unwilling to follow ROSENBERG in his theory of reduction.

For these reasons the writer believes that the mitoses in the oogonia and antheridia of the Phycomycetes have no special significance, or are merely the remains of nuclear divisions that were formerly characteristic of simpler types of gametangia or perhaps the primitive sporangia that preceded these.

The simple precesses of oogonesis in Vaucheria seem to prove conclusively that all of the nuclei in the oogonium are homologous and potentially gamete nuclei, and this supports HARTOG'S suggestion for Saprolegnia of many years ago. The author believes this to be equally true of the nuclei in the gametangia of the Saprolegniales and the Peronosporales. The mitoses in the last two groups have complicated the problem, but there seems now to be no special significance in these divisions, since they are not only variable in number, but may be entirely absent. Thus there are two mitoses in Albugo and Plasmopara, but only one in Saprolegnia, certain species of Peronospora, and Pythium, and they are entirely absent in the species of Vaucheria just described.

There are then excellent reasons for considering all of the potential and functional gamete nuclei in Vaucheria, Saprolegnia, and the Peronosporales as homologous, and there seems to be little doubt but that the oogonia of all these forms are related at least as gametangia through remote ancestors, if not as fully differentiated oogonia.

The problems then concern the exact relationships between the eggs of Vaucheria, Saprolegnia, and forms of the Peronosporales. Are these female gametes strictly speaking homologous, or have they been developed along somewhat different paths? An old view, and that probably held by most botanists, is one of strict homology, implying an intimate relationship between these fungi and Vaucheria. It is a problem of fundamental importance in all discussions of phylogeny in this region of the plant kingdom, and of special concern to those who make Vaucheria the starting point of a series of fungi beginning with the Peronosporales or the Saprolegniales and ending in the Mucorales.

From all points of view oogenesis in Vaucheria is simpler than in the Saprolegniales or Peronosporales. It conforms perfectly to well-known principles of sexual evolution which the author has recently discussed (*Popular Science Monthly*, February 1903, p. 300). The process represents the final stage of nuclear reduction in a multinucleate oogonium, and indicates plainly that the ancestral gametangium produced numerous gametes which were undoubtedly motile, since the sperms of Vaucheria are biciliate and the Siphonales reproduce almost universally asexually by zoospores. It is difficult to follow exactly the steps through which the ancestors of Vaucheria passed in their evolution from isogamy, because it is the only heterogamous type in the order, and there are few connecting links with the prevailing simple conditions among the Siphonales. However, we have in Bryopsis a form whose gametes, although both motile, are of different sizes, those of the female being much larger and developed less numerously in the gametangium. This type exhibits the first step toward the condition of heterogamy, but we do not know exactly what would follow next. Probably the protoplasmic cleavage in the female gametangium would become gradually reduced and fewer gametes formed, until finally there would be no more cleavage, all of the protoplasm going into a single gamete, which when non-motile would become the solitary egg (Vaucheria). This concentration of protoplasm for a lessened number of gametes or for a single egg must be accompanied by nuclear degeneration *if the ancestral gametangium were multinucleate.* There are of course types of gametangia among the algae which are uninucleate from the beginning, and there cannot be any nuclear degeneration in these. But the multinucleate gametangium is not uncommon in certain groups, and is apparently universally present in the Siphonales.

It is possible that Sphaeroplea will be found to represent a stage in sexual evolution intermediate between Bryopsis and Vaucheria, without necessarily implying a relationship to these types. Klebahn ('99) and Golenkin ('99) have given us the most complete accounts of oogonesis in Sphaeroplea. Klebahn found the eggs of *S. annulina Braunii* to contain several nuclei (2–5), one of which became the functional female gamete nucleus; the others remained inactive and might be found in the ripe spore. It becomes an interesting question whether or not these would eventually degenerate. This form of Sphaeroplea may illustrate the beginning of a process by which fewer eggs are developed than the number of gamete nuclei, but before a habit of nuclear degeneration has become fully established. It is altogether probable that the extra nuclei in the eggs of the var. *Braunii* do eventually break down.

Besides Sphaeroplea, it is very important that we know the processes of oogenesis in Monoblepharis, since this form has a structure with many points of resemblance to the algae on the one hand and the groups of Saprolegniales and Peronosporales on the other. LAGERHEIM ('00) states that a single large nucleus enters the developing oogonium to become the gamete nucleus of the egg. Such a history is not in sympathy with oogenesis in Vaucheria and the Peronosporales or Saprolegniales, nor is it in sympathy with his own description of spermatogenesis in Monoblepharis. The antheridium contains many nuclei, each of which enters into the development of a sperm as in Vaucheria. The author cannot but think that LAGERHEIM'S account of oogenesis is incorrect, or else that the conditions here are very exceptional. It seems very probable that Monoblepharis and perhaps some of the forms in the Leptomitaceae are closely related to Vaucheria.

The problem of the relationship of the events of oogenesis in the Saprolegniales and Peronosporales to Vaucheria may be stated as follows. Have the conditions in these groups been developed directly from the relatively simple process illustrated by Vaucheria, or are there peculiarities in these two groups that would make necessary their derivation from more generalized types?

The Saprolegniales present conditions that superficially bear a very close resemblance to Sphaeroplea, *i. e.*, there are several eggs in the oogonium. But these eggs are differentiated around coenocentra which determine the survival of a limited number of nuclei, while the great majority break down. There are fundamental differences between these events and oogenesis in Sphaeroplea, unless later studies should establish nuclear degeneration in the latter type. It would not be difficult to conceive the development of several metabolic centers in a large gametangium of one of the Siphonales, and the survival of several nuclei to form as many eggs which would give a condition exactly like that of Saprolegnia. So the present investigation with the discovery of a multinucleate oogonium in Vaucheria tends to bring the Saprolegniales into a somewhat close relationship to Vaucheria, not directly of course, but probably through more generalized types of the Siphonales now extinct.

The Peronosporales offer a more difficult problem than the Saprolegniales, yet there are fundamental features of oogonesis here in agreement with this group and with Vaucheria, namely a multinucleate oogonium and extensive nuclear degeneration. The advance of the process of oogenesis in the Peronosporales over that of Vaucheria lies in the differentiation of ooplasm and periplasm, the first being associated with a remarkably well-developed coenocentrum. The influence of this coenocentrum determines the survival of one or more nuclei in the ooplasm to give a uninucleate or multinucleate egg. The periplasm, containing numerous nuclei, becomes separated from the ooplasm, and although assisting in the deposition of the oospore wall its nuclei and cytoplasm finally become disorganized.

The processes of oogenesis in the Saprolegniales and Peronosporales seem higher than those of Vaucheria because of the remarkable activities of the coenocentra. But to derive the sexual organs of the first two groups from the last form, it would be necessary to postulate the suppression of two important activities in Vaucheria, namely, the development of motile sperms and the formation of pores in the gametangia for the entrance and exit of these structures. The suppression of the pore formation and consequent modification of the sexual cells, the establishment of several coenocentra in the Saprolegniales, and the specialization of a periplasm in the Peronosporales are peculiarities involving very important protoplasmic activities not represented in Vaucheria.

We have in the Saprolegniales and Peronosporales the interesting association of complex female organs developing eggs, with male organs that are much simpler. The antheridia in the first two groups are all mutinucleate and morphologically gametangia. In certain forms (*Albugo Bliti* and *A. Portulacae*) the antheridia are actually coenogametes as truly as those of the Mucorales, because large numbers of functional gamete nuclei are discharged into a multinucleate egg. Uninucleate gametes, probably motile in ancestral types, have been given up, and the antheridium, acting as a unit, follows the chemotactic tendencies of a male sexual cell in its fusion with the female. All of these antheridia behave in the same manner whether there are one or many functional gamete nuclei. This condition must have been closely associated in its origin with the suppression of the habit of forming pores for the discharge of zoospores or motile gametes.

We do not know enough about the pore-forming activity in zoosporangia and gametangia to understand how readily it may be given up, and whether its presence or absence is of great morphological importance. The activity is absent in the gametangia of the Mucorales, Saprolegniales, and Peronosporales, but present in the sporangia of the Saprolegniales and most Peronosporales (conidia which produce zoospores), although lacking in some forms (Peronospora and certain species of Pythium) whose conidia germinate by a tube. The sporangia of the molds may have at one time developed zoospores, but there is at present no hint of such possible activities, except a general agreement in the processes of protoplasmic cleavage by furrows with spore-formation in such zoosporangia as have been studied (Hydrodictyon, Saprolegia, etc.).

If the suppression of the pore-forming activity may take place readily after some slight change in life-habits, there would seem to be no great difficulty in relating the processes of oogenesis in Saprolegnia and the Peronosporales rather closely to Vaucheria or relatives of Vaucheria. But if pore-formation may be given up only under exceptional conditions and infrequently, then it becomes very questionable whether there can be a close relation to Vaucheria, and we must look to another line of ancestry for the Saprolegniales and Peronosporales. The author thinks the latter condition at least quite possible and deserving of further consideration.

Such an ancestry for the Saprolegniales and Peronosporales would naturally be sought through simpler conditions, somewhat like those illustrated in the Mucorales whose gametangia are coenogametes. It is scarcely conceivable that the molds are very closely related to the first two groups, but their coenogametes illustrate such well-defined sexual conditions that they naturally enter into the discussion. It is possible that groups with coenogametes like those of the molds might gradually differentiate such structures until they would finally become male and female sexual organs. The female coenogamete would be larger and well supplied with food material, and might finally develop one or more eggs and thus become an oogonium; the male coenogamete in contrast would remain small or perhaps become further reduced and would be called an antheridium when it bore a sexual relation to an oogonium. Thus conditions like these of the Saprolegniales and Peronosporales might arise from coenogametes resembling those of the molds, and a condition of heterogamy result, which would closely resemble that of Vaucheria and yet have no genetic relation to the latter condition. The eggs of the Saprolegniales and Peronosporales in such an event would have an origin entirely independent of any other line of sexual evolution, and with the conspicuous peculiarity of coenocentra marking the position of dynamic centers during the process of oogenesis.

A question sure to be raised in this connection is the possibility of undifferentiated coenogametes of the mold type arising through the simplification or degeneration of organs like the antheridia and oogonia of the Saprolegniales and Peronosporales. Such a line of evolution would demand the suppression of some very highly differentiated cell processes, such as the extensive nuclear degeneration, the formation of coenocentra, and the differentiation of periplasm. There is no evidence of such tendencies among the forms in question, but, on the contrary, excellent reasons for believing that the direction of sexual evolution is toward greater and more precise protoplasmic complexity rather than simplification. The point is especially well illustrated in the series of species in the genus Albugo, where the line is clearly from the multinucleate egg and small coenocentrum of *A. Bliti* to the uninucleate egg and extraordinary large coenocentra of *A. candida* and *A. Lepigoni*. The author can see at present no probability of a line of sexual degeneration or simplification from higher forms toward the molds.

For these reasons we are driven to consider the possibility of an origin of the coenogametes of molds from gametangia that have not passed the stage of isogamy. I have previously (DAVIS '00, p. 308, and '03, p. 335) advanced the hypothesis that such coenogametes may have arisen from gametangia somewhat like those now found among the lower Siphonales and in Cladophora. These gametangia are generally terminal structures that discharge motile gametes.

But should organisms of this type (whether algae or fungi) be placed under conditions unfavorable for the formation of motile gametes, the gametangia themselves might be expected to act as coenocytic units, and obeying the chemotactic influences of sexual cells fuse with one another as coenogametes.

So the problems of phylogeny in this higher region of the Phycomycetes become greatly complicated through factors that concern the environment and life-habits of the forms in question. The absence of pores in structures that at one time evidently formed motile gametes presents great difficulties to the establishment of relationships between the Mucorales, Saprolegniales, Peronosporales, and Vaucheria. Yet, it may be that the suppression of this structure indicates little more than a change in life-habit from an aquatic to an aerial existience (Mucorales) or to a parasitic life (Peronosporales), with the apogamous Saprolegniales presenting conditions peculiar to themselves. But until we know more about these life-habits and the possibility of an organism passing from one condition into another, it is pure speculation to lay out lines of relationship. And again, we lack knowledge of the processes of oogenesis in a number of forms which may have important bearings on these problems of phylogeny (especially for Monoblepharis and Sphaeroplea).

In spite of the complications of the problems of phylogeny in the Phycomycetes, certain features stand out clearly which may be briefly summarized. The multinucleate character of the sexual organs in types of the Mucorales, Saprolegniales, and Peronosporales thus far studied, and perhaps some other forms as well (Monoblepharis) is likely to prove universal in these groups. Numerical reduction of potential gamete nuclei takes place through degeneration, a process of great physiological interest which deserves careful study. The suppression of the pore-forming activity gives the closed oogonium and antheridium peculiar to the fungal groups. The coenogametes characteristic of the Mucorales and also illustrated by certain of the Peronosporales (*Albugo Bliti*, *A. Portulacae*) are morphologically gametangia and probably have had their origin by the suppression of the processes of cleavage to form many gametes and their assumption as coenocytic units of sexual attributes. The Saprolegniales and Peronosporales exhibit the further peculiarity of eggs differentiated around dynamic centers (coenocentra), with the specialization of a periplasm in some forms. Perhaps the highest expression of periplasmic development is the cellular envelope which finally invests the egg of Araiospora.

SUMMARY OF THE INVESTIGATION OF VAUCHERIA.

The oogonium arises as a process containing dense protoplasm with many plastids and nuclei. As the young structure increases in size, vacuoles develop in the protoplasm, which consequently forms a peripheral layer next the cell wall.

The number of nuclei is variable, but always large, probably ranging from 20 to 50. There are no mitoses in the oogonium.

The oogonium becomes separated from the parent filament by a cross wall which is developed between two plasma membranes that appear to be formed along the surfaces of flattened vacuoles.

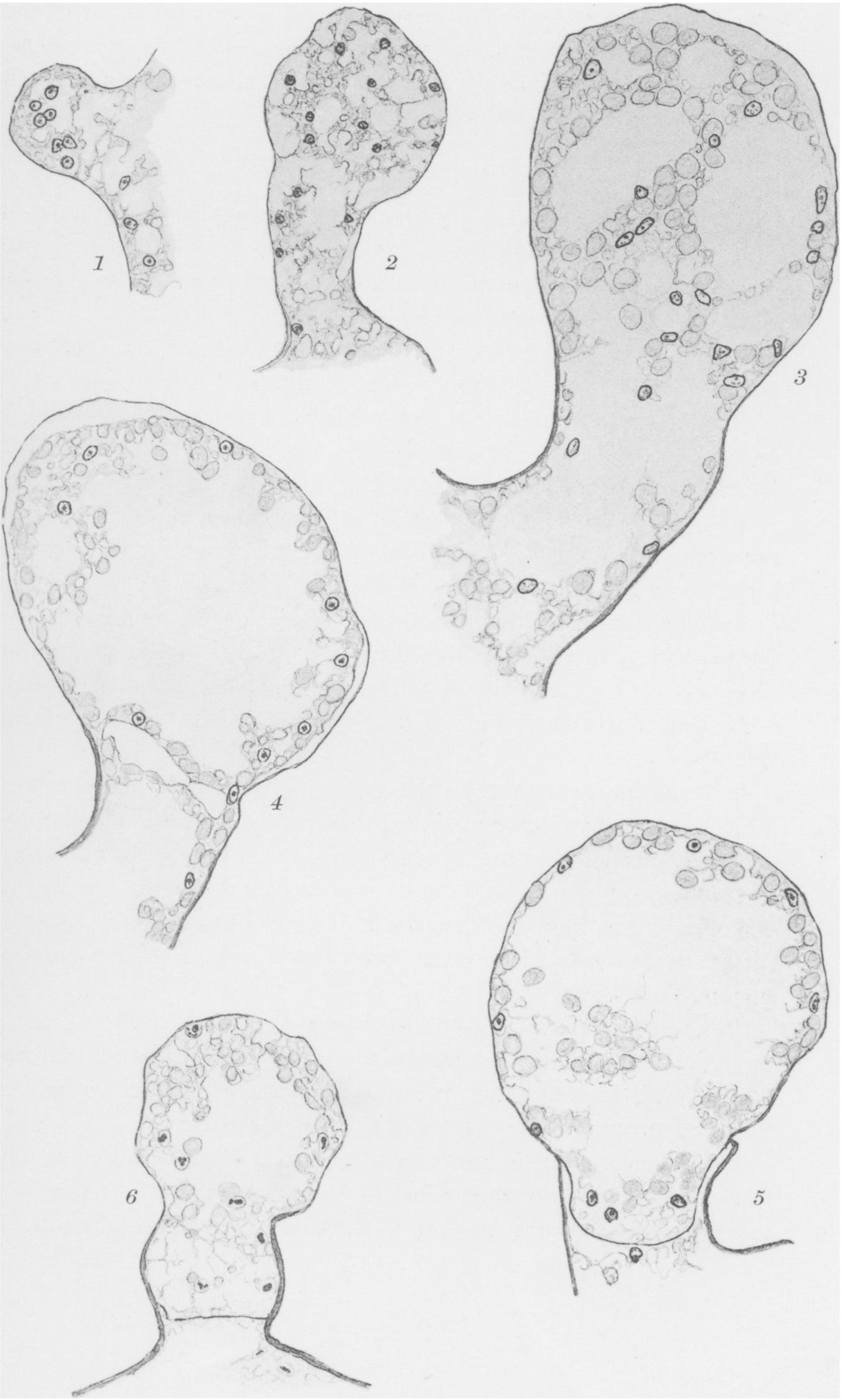
The oogonium is multinucleate at the time the cross wall is formed; but even then there is evidence of the degeneration which becomes much more pronounced later.

In older oogonia the degenerating nuclei are found chiefly in the periplasm. They become exceedingly small, the nuclear membrane disappearing first, and finally nothing remains but granular matter, apparently nucleolar, which is finally lost in the cytoplasm of the cell.

A single nucleus survives the general processes of degeneration. This becomes the gamete nucleus and takes its position near the center of the egg, which is probably the situation most favorable for its growth. There is apparently no coenocentrum in the egg of Vaucheria, but the surviving nucleus frequently lies in a mass of rather dense protoplasm which may readily represent a center of metabolic activity.

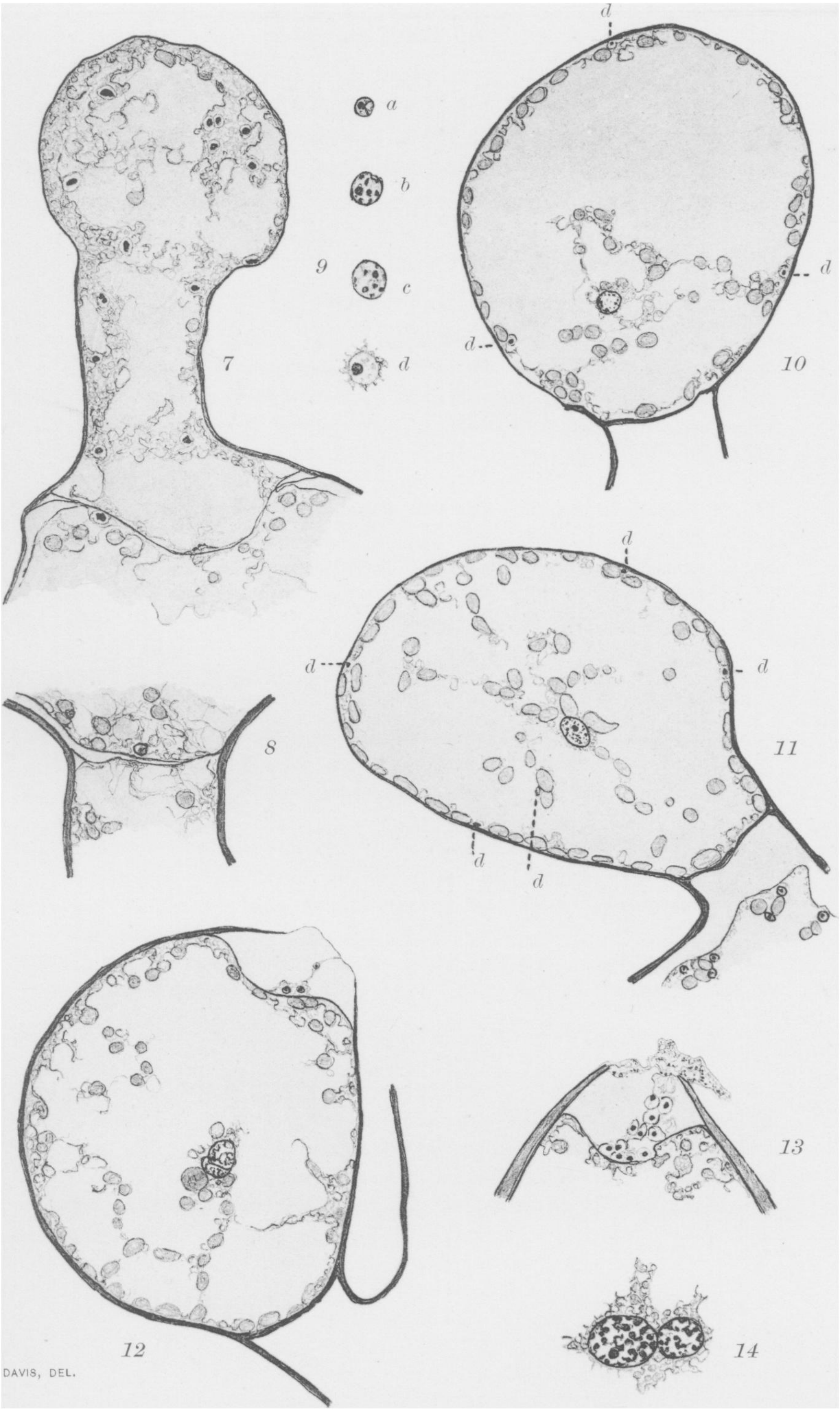
There are excellent reasons for believing that all of the nuclei in the young oogonium are potentially gamete nuclei, and that the selected egg nucleus owes its survival and later growth entirely to the good fortune of a favorable situation in the cell.

The gamete nucleus grows rapidly until it is finally three or four times the size of the nuclei in the young oogonium. There is a marked increase in the amount of chromatin, which fills the interior



DAVIS, DEL.

DAVIS on VAUCHERIA.



DAVIS on VAUCHERIA.

of the nucleus with numerous small granules on a delicate linin network.

After fertilization the nucleus of the sperm passes to the center of the egg, where it increases in size at the side of the female nucleus in the same region of dense protoplasm. The two sexual nuclei fuse slowly when both are approximately of the same size.

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EXPLANATION OF PLATES VI AND VII.

The sections were cut 5 μ thick and stained with safranin and gentian violet. All figures were sketched with an Abbé camera under the Zeiss apochromatic objectives 2^{mm} or 1.5^{mm} in combination with compensation oculars. The magnification is as follows: *figs. 1–2*, ×500; *figs. 3–8* and *10–13*, ×667; *fig. 9*, ×2,000; *fig. 14*, ×1,334.

FIG. 1. Oogonium beginning to develop.

FIG. 2. Young oogonium.

FIG. 3. Young oogonium, large vacuoles forming.

FIG. 4. Oogonium, flattened vacuoles marking the positions where the cross wall would have been formed.

FIG. 5. Oogonium, delicate cross wall just formed.

FIG. 6. Oogonium, delicate cross wall, nuclei showing signs of degeneration.

FIG. 7. Oogonium, cross wall, nuclei degenerating.

FIG. 8. Cross wall between two plasma membranes.

FIG. 9. A series of nuclei from the same section to illustrate the process of degeneration with the gradual disappearance of the chromatin and the fading of the nuclear membrane: *a*, from antheridium; *b*, from just below the antheridium; *c*, from near the oogonium; *d*, from within the oogonium.

FIG. 10. Old oogonium with gamete nucleus in the central mass of protoplasm and degenerating nuclei (*d*) in the peripheral layer.

FIG. 11. Oogonium older than *fig. 10* and probably mature, remains of degenerating nuclei (*d*) in the peripheral layer of protoplasm.

FIG. 12. Fertilized egg, gamete nuclei fusing in a mass of dense protoplasm.

FIG. 13. Tip of oogonium showing mass of sperms in the slime at the opening.

FIG. 14. Gamete nuclei showing comparative size and general similarity in structure when about to fuse.